

Saproxylic Beetles

Subjects: Forestry

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Saproxylic beetles are dependent on dead wood at any stage of their own development and at any stage of wood decomposition e.g. mycetophages on wood-decay fungi. This group of saproxylic beetles has become a frequently used as a bioindicator of forest biodiversity.

Keywords: saproxylic beetles ; deadwood ; integrated forest management ; deadwood enrichment ; species richness ; managed stands

1. Introduction

The importance of deadwood for the biodiversity of saproxylic species of insects and fungi, as well as for the natural functioning of forest ecosystems, has long been the subject of research. Over the last 20 years, this topic has become the focus of attention for commercial forests too, as deadwood is no longer seen as a product of poor forest management. However, this issue has not been comprehensively settled in order to be a tangible and acceptable forestry practice. To date, there have been isolated research studies ^{[1][2][3]} or various original experiments, e.g., ^{[4][5][6][7][8]}. Saproxylic organisms are dependent on deadwood at all stages of their development, and throughout any stage of wood decomposition ^{[1][9][10][11]}. The largest groups bound to deadwood are fungi and insects ^{[12][13]}. Fungi are the most important factor in the decomposition process ^{[14][15]}, especially the division Basidiomycetes ^[16], and insects are the most important vector with active wood-seeking movement, while their way of life helps to spread fungi to more distant places ^{[17][18][19]}. Saproxylic beetles are very popular because they provide reliable data on the preservation of the environment and are often used as indicators of forest biodiversity ^{[2][9][13][20][21][22]}. Nature reserves are one of the options to preserve and create conditions for many specific species of animals. A forest area excluded from management, however, may not always be the most advantageous environment for saproxylic beetles. In this respect, suitable habitats for a non-intervention regime are found especially at higher and middle altitudes in stands predominantly consisting of three main tree species—Norway spruce, European beech, and silver fir ^[23]. The non-intervention regime is also suitable for extreme positions, steep slopes, and drying sites where the canopy is not fully closed, and the stands remain strongly differentiated ^[24]. Nevertheless, a conservation (non-intervention) strategy is inappropriate for lowland forests where local species depend on sunny habitats, e.g., oak forests ^{[25][26]}. The absence of management would lead to the homogenization of species composition, the closure of the canopy, and a strong reduction of species richness of saproxylic beetles ^{[24][27][28][29][30][31][32][33]}. In addition, there are a number of typical attributes of the natural forest in the reserves, towards which the development spontaneously leads. In particular, we are talking about large volumes of coarse woody debris (CWD), spatial heterogeneity, and the limited use of tree species, among other factors ^[4]. Societally, these facets are mostly considered as beneficial, but the owners to some extent view them as negative ^[4]. It is the wood production function that the owners perceive as positive, while it is excluded in nature reserves. Therefore, a compromise is sought between wood biomass production, and the expansion of the typical characteristics of natural forests, as high volumes of deadwood are problematic for the economy of forest enterprises ^[34]. One way to combine the production functions of forests and high biodiversity is functionally integrated forest management, with an emphasis on active enrichment of stands with deadwood ^[6], or retention management, which is preferred in Scandinavia, e.g., ^[35]. The implementation of different methods of management depends on several factors: socio-cultural, economic, and political ^[36]. In contrast to nature reserves, the goal of silvicultural interventions in functionally integrated forest management is the gradual increase in stand volumes and the improvement of production quality, accompanied by active enrichment with wood necromass ^[37]. Active enrichment with wood necromass may be in fact faster than the natural increase of deadwood volumes in newly established reserves ^{[4][5][6][7]}. While conventional forest management reduces the amount of deadwood, the number of microhabitats and the diameter differentiation of trees ^[37], functionally integrated management seeks to take into account all of these attributes ^[4]. However, it must be remembered that in commercial forests, it is still necessary to observe the basic principles of forest protection and the struggle against pests with special regard to climate change, reflected in rising temperatures and the uneven distribution of precipitation—including periods of intense drought, which has manifested itself over the last years in Central Europe. These factors induce long-term stress on forest stands,

reducing the natural resistance of forest tree species, and conversely, increasing the risk of an outbreak of insect pests, e.g., [38][39][40][41].

The application of scientific findings on the importance of deadwood in the management of production forests, which form the main share of woodlands in Central Europe, is essential for the biological diversity in the wider region of forests. Based on a thorough analysis of scientific findings, this work aims to define the attributes of functionally integrated forest management supporting the biological diversity of the saproxylic beetle species. The goal is to propose appropriate management measures in the context of common forestry practice in the Central Europe region.

2. What Is the Optimal Constant Volume of Deadwood?

Discussions are often held on the amount of deadwood left to decompose, which is needed to comprehensively fulfill all its functions, while at the same time balance the reproductive offer for the widest possible range of saproxylic beetles. This question is important for the planning of wood-necromass management, as the number of saproxylic beetles are known to increase with the amount of deadwood [6][42][43][44][45][46][47][48] and wood-inhabiting fungi [23][49][50]. The number of large logs in the late stage of decay, and the constant volume per hectare are the variables that best explain the species richness of this group of beetles [51][52][53] and fungi [50]. With each m³ of deadwood per hectare, the number of saproxylic beetle and fungal species increases on average by an additional 1.2 species [5]. To some extent, even the exact optimal volume is relative, as it encounters acceptable economic loss and other risks associated with deadwood [1]. In some published studies, we can find a specified universal volume of deadwood for increasing and maintaining the biological diversity of saproxylic beetles in commercial forests. This volume most often fluctuates between 20 and 60 m³/ha [34][54][43][55][56].

These values correlate to the diversity of wood-decaying fungi, for which the optimal volume of deadwood might exceed 100 m³/ha, and only from 20 m³/ha do the first endangered species begin to appear [57]. Wood-decaying fungi generally require high volumes of necromass, sometimes exceeding 300 m³/ha [23]. Many saproxylic beetles are linked to wood-decaying fungi [7][17][58][59]. The solar influence is essential for the abundance and diversity of saproxylic beetles [28][60][61], and at the same time, sun exposure can compensate for the amount of deadwood [23]. A greater amount of insolation in sunny stands reduces the required volume of deadwood for saproxylic beetles, and vice versa in shady cold stands [43][62][63]. The strength of the effect of sun exposure on species richness of saproxylic beetles is more likely related to the local climate—the importance of sun exposure diminishes and may not become a limiting factor in warmer climatic conditions. By contrast, wood-decaying fungi react negatively to changed or opened canopy [23]. Humid and warmer environments are very important factors for many fungal decomposers [49][64][65]. Thus, in the case of high volumes of deadwood, sun exposure may be a limiting factor for biodiversity [44]. At the same time, several large logs cannot be replaced by a larger number of thin logs or even smallwood [66]. Logs are more valuable than branches [45], as numerous species cannot live on small dimensions of dead biomass and have a set minimum threshold diameter [45][67]. Similarly, the number of saproxylic beetle species increases with biomass diameter [68][69].

If we compare these recommended volumes of deadwood in managed stands to the current state of forests in 19 European countries, where there is an average of 15.6 m³/ha of deadwood, we find significant differences [70]. More precise volumes of deadwood identified in commercial forests are given in **Table 1**. The small volume of deadwood is the main reason why commercial stands are very poor in saproxylic beetles [54][71][72]. The same applies to the most endangered species in forest ecosystems, where these volumes are well below the limits at which they begin to appear [54], e.g., typically over 60 m³/ha [34][44][62].

Table 1. Volume of deadwood in managed stands (m³/ha).

Volume (m ³ /ha)	Tree Species	Country	
Fridman and Walheim (2000) [73]	6.1	Coniferous	Sweden
Siitonen (2001) [74]	14	Coniferous	Finland
Christensen et al. (2005) [75]	10	Beech	Europe
Vašíček (2007) [76]	5.5–9	Mix	Czech Republic
Vítková et al. (2018) [3]	9.1	Mix	Czech Republic
Puletti et al. (2019) [70]	9.8	Mix	Czech Republic

Volume (m ³ /ha)	Tree Species	Country	
Roth et al. (2019) ^[7]	18.9	Beech	Germany
Kučera and Adolt (2019) ^[77]	6.7–13.8	Mix	Czech Republic
Leidinger et al. (2020) ^[8]	19.3	Beech-oak	Germany
Bujoczek et al. (2021) ^[78]	4.1–15	Mix	Poland

Tree species—the main tree species occurring in studied forest stands. Mix: forest stands with coniferous and deciduous tree species combined.

Up to three times higher volumes of deadwood were detected in commercial stands in mountain areas ^[78]. However, even this condition strongly limits the biodiversity of saproxylic beetles because in such cold locations, a higher volume of deadwood is required compared to warm ecosystems ^{[43][62]}. The diversity of deadwood is also important ^[63]. Increased volumes of deadwood—and consequently, the saproxylic beetles' diversity—are highly correlated with the diversity of other taxonomic saproxylic groups, which leads to an increase in the overall multidiversity of saproxylics ^[74]. This is due to the inhabitation of the same or similar types of deadwood microhabitats, e.g. by fungi, lichens, and mosses ^{[34][50][79]}, also the group of Diptera ^[80]. This is also confirmed by the proven causality in the number of nesting birds in tree snags only when robustly colonized by saproxylic beetles ^[81].

3. How to Effectively Enrich the Stands

It is simple to enrich the stands just by leaving the felled logs, felling residues, and fallen wood in place ^[1]. The enrichment of forest stands with only small fractions of wood biomass is insufficient in terms of increasing biodiversity ^[3]. It is necessary to focus on bulky specimens of deadwood, as this type of wood is certainly missing in the commercial stands ^[82]. Therefore, thick wood fractions need to be applied ^{[2][83]}. The minimum diameter is 15 cm ^{[84][85]}, but at the same time, the increasing diameter of deadwood increases the possibility to host bigger species of beetles ^[45] and a larger number of saproxylic beetles ^[69] and fungi ^[50]. Also, Grossner et al. ^[34] recommend preserving deadwood of larger dimensions in the stands, with a diameter of 50 cm and more, as much as possible. Primeval forest relics, which are species that depend upon forest habitats without interrupting the continuity of the forest with large amounts of bulky (>40 cm) deadwood ^{[11][86][87][88][89][90]}.

Diameters over 70 cm of veteran trees have a demonstrably positive effect on all saproxylic beetles ^[44]. Sizeable deadwood deposits can host more saproxylic species, both endangered and common, simultaneously ^[91]. However, such large fractions are very scarce in forests ^[92], while they are essential for highly endangered and rare saproxylic beetle species ^{[11][34][56][83][89][90]}. Although smaller wood necromass also hosts many saproxylic beetles ^{[69][93]}, these are mainly groups of common species ^{[56][93]}. However, some studies still favor smaller deadwood mass over large fractions ^[94]. The difference is probably due to the greater abundance of early species of saproxylic beetles rather than the later species, which are dependent upon the later stages of wood decomposition.

Active enrichment brings about a more complicated issue—standing deadwood, the so-called snags, or microhabitat trees ^{[4][5]}. Good results in terms of biodiversity are provided by so-called ring-barked trees ^[95] or stumps of up to 4 m high (**Figure 1**), often used and studied in Scandinavian countries ^{[35][96][97][98]}. High stumps are parts of the trees that remain in the stand after they have been felled at a greater height. Normally, trees are felled at a height just above the ground utilizing the lower part of the trunk to produce wood products. The importance of standing deadwood and its greater impact on biodiversity than that of lying logs, especially in endangered species, is illustrated in many cases ^{[52][66][84][99][100]}. They carry the highest number of microhabitats per unit area ^[101]. For this reason, it is necessary to focus on standing deadwood. The simplest, safest, and at the same time the most economically viable way seems to be the formation of high stumps, when at this height, we can then talk about the equivalent of snags. Nevertheless, leaving live trees in the stands is the most frequently recommended method ^[1], even though there is a far greater safety risk due to the unpredictable fall of a dying tree ^[3]. Leaving live coniferous species in commercial stands does not develop high-quality microhabitats for saproxylic organisms even after an extended period of time. It is much more convenient to leave deciduous tree species to die naturally in the stands ^[102] due to their high potential for microhabitat formation ^{[3][103]}.

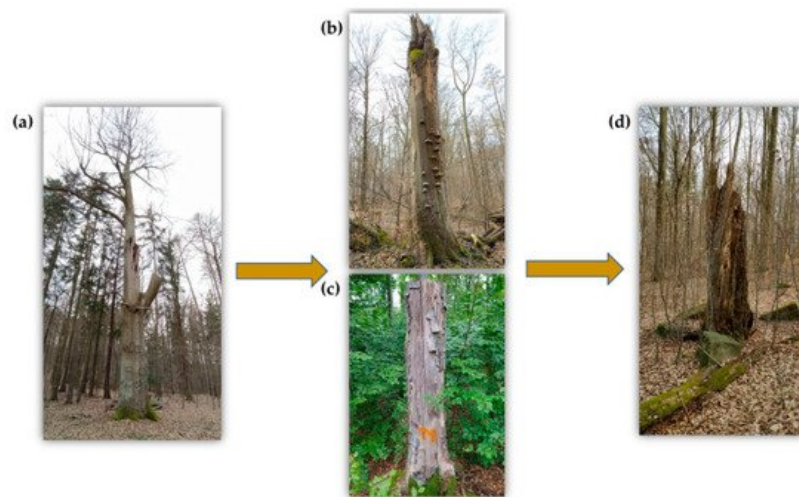


Figure 1. Development of a veteran tree. (a) Solitary tree, which is slowly approaching the limit of physical age and creates a variety of microhabitats. (b) The snags are very valuable for saproxylic beetles. (c) The man-made snags (high stumps) are a suitable substitute in places where trees cannot be left to develop spontaneously. (d) Very advanced stage of decomposition process of the snags.

In high stumps, it will take longer for the wood to become attractive to saproxylic species of the later stages of the decomposition process, because the decomposition of higher stumps takes longer [65]. In some cases, decomposition took up to 3 times longer, and was due to substantially lower moisture of the snag's wood [73][104][105][106]. The point of the attractiveness to beetles was confirmed by Jonsell and Weslien [96]. It was found that even man-made stumps that are several years old match the species richness of natural stumps [97]. For species of the early stages of deadwood decomposition, insolation is more important than the diameter of the stump [98]. As the decomposition phase of deadwood progresses, the species dependent on these stages of deadwood decomposition will also occur [17]. With larger dimensions, however, deadwood in the form of trunk torsos and high stumps can host more microhabitats such as cavities, and thus be a hotspot for saproxylic beetles as well as nesting birds and bats. The larger the diameter of the tree, the more species of common and endangered beetles [107][108][109], as well as *Picidae* birds are found [81]. By contrast, fungi prefer lying deadwood [50].

It has been confirmed that the volume of lying wood has effectively increased since the introduction of integrated management, but special support for standing deadwood is still a necessity. Even after the introduction of integrated management, the number of torsos has not increased, while habitat trees have even decreased [4]. The share of standing deadwood is 20–30% (mode) of the total volume of deadwood, exceeding 100 m³/ha. This share was found in natural forests and old reserves [75][101][105][110][111][112]. Too many snags on the local level (e.g., in one stand) can reduce the occupancy of individual snags, as resource availability would be greater than the ability of beetle communities to colonize these habitats [95]. At the same time, keeping in mind that isolation is negative, it is important to maintain the connection between these habitats [108], preferably in groups [2]. Functionally, the trunk torsos and veteran trees are also suitable for biological forest protection due to their great host potential. They often host large numbers of predatory, parasitoid insects, birds, and bats, and the synergistic effect of these groups can inhibit the growing number of pests to some extent. Deadwood itself is the host of many pest antagonists [84]. The enrichment strategy and the subsequent change over several years were evaluated by Doerfler et al. [5], who found that deadwood mass in production forests increased from 8 m³ (set 1) and 18.9 m³ (set 2) to 13.6 m³ and 67.9 m³ (set 1 ≥ 20 cm, set 2 ≥ 12 cm of deadwood for timber inventory). In standard production management, the annual increase in the average level of deadwood is only 0.18 m³/h [73]. As a result of active enrichment, saproxylic species respond positively to the increased amounts of deadwood in stands [5][6][7][113] and simultaneously increase multidiversity, including non-saproxylic insect species [5]. It has even been found that the biodiversity of the saproxylics in production stands has exceeded recent reserves [8], or at least equalized them [7]. This can be proof of how suitable integrated forest management is for supporting an abundance of insects without the need for permanent and strict conservation activities that exclude the production function of forests. A positive effect of close-to-nature integrated management on saproxylic beetles is also confirmed by Jacobsen et al. [114].

4. Maintaining Constant Volume Continuity

The continuity of deadwood over time is essential for the maintenance of biodiversity, so that the supply of microhabitats for invertebrates is constantly evolving and emerging [46][115][116]. If a species does not find their particular type of microhabitat to establish in the landscape, they will persist in their current location, and upon losing it, they will completely

disappear and become regionally extinct ^[117]. Therefore, it is necessary to supply deadwood more often than only once during the entire production period (rotation), as the decomposition process of wood is relatively short in some cases. The metadata assessment shows that wood of European beech (*Fagus sylvatica*, L.) decomposes fastest, in 20–60 years. The wood of Norway spruce (*Picea abies*, L. H. Karst) decomposes within 50–100 years on average, and wood of silver fir (*Abies alba*, Mill.) within 70–110 years, depending on the conditions and dimensions ^{[64][65][105][106][118][119][120][121][122][123][124][125]}. By contrast, oak (*Quercus* sp.) is rather stable, and its wood standardly decomposes for at least 90 years in all circumstances ^[126].

For this reason, it is necessary to carry out the enrichment at least three times within the European beech rotation period, two times in the case of Norway spruce, and once is sufficient for the average oak rotation period, which is 115 years in the Czech Republic (Information on Forest and Forestry 2019). Similarly, enrichment in the range of 25–40 years is recommended by Přívětivý et al. ^[64]. Alternatively, it is recommended to keep standing trees in the stand to decay naturally, to bridge the period when deadwood is not left purposely in place after regeneration felling ^{[1][3]}. In order to create a practical methodology for forest owners—in connection with financial compensation—it will be necessary to calculate in more detail the necessary enrichment phases according to the site conditions and their original rotation periods.

5. Discussion and Conclusions

The proposed management model suggests a relatively rapid enrichment of stands with deadwood, which is a key factor in increasing the diversity of saproxylic organisms. At the same time, the production function of forest stands—and thus the use of wood is not suppressed. Management is designed to be applicable to current standard forest management models. However, it is obvious that alternative, close-to-nature silvicultural methods are also important for increasing biodiversity in commercial forests. Changing silviculture systems are creating different conditions for many invertebrate communities continuously present in forest stands. In our study was calculated volume of dead wood at 40–60 m³/ha. This is a volume attempting to balance a wide range of requirements for saproxylic beetles, other ecosystem functions and economic considerations. This volume will ensure the survival of many endangered species, with the exception of critically endangered primeval forest relics. The actual enrichment process is assessed in relation to the rate of decomposition of the examined tree species deadwood, and on the models of tending and regeneration silviculture measures. The most intensive management model is designed for beech stands (150 m³/ha per rotation period), while the least intensive enrichment is designed for oak stands (50 m³/ha per rotation period). Enrichment during the stand development is shifted to more advanced stages, when it is possible to leave wood of larger dimensions in the stand, which is especially important for increasing the diversity and abundance of rare species of saproxylic beetles. Deadwood over 15 cm of diameter has the best properties. These larger fractions maintain suitable conditions for extended periods of time. Standing deadwood should be kept in groups, with at least a few individuals representing a share of 20–30% of the total volume of deadwood. High stumps are available and safe standing deadwood. Due to economic aspects, labor intensity, and the effect on biodiversity, it is clear that creating such high stumps should be performed on trees with diameter at breast height (DBH) >35 cm. When created by harvester technology, even occupational safety precautions are met. In terms of the diversity of dead biomass, it is necessary to naturally preserve dead trees and their parts, as they are often damaged and contain important microhabitats—provided that there is no threat to forest stands by pests. This type of deadwood can be expected in the longer term from the trees that will be left standing to die naturally in the stand. However, the forest manager will find it difficult to select convenient places where these unique trees can be left to die naturally. Suitable sites include places where a substantial loss of the stand-growing area does not pose a problem, and where no significant crown projection is an obstacle to the growth of the new forest. From a safety perspective, it is necessary to avoid places frequently visited by people. A continuity of nutrient/residence stability is undoubtedly a key issue. To maintain stability, it is necessary to enrich several times during the rotation period, depending on the type of species. It is three times for *F. sylvatica*, two times for *P. abies*, and once for *Quercus* sp. during their rotation period. In terms of standing wood, the production of high stumps in regeneration felling will be combined with leaving several live trees in place to die naturally. The starting point of functionally integrated management is not tied to specific sites or conditions. This management concept can be used almost wherever the diversity of the landscape is observed. However, from the point of view of saproxylic beetles with rather limited mobility, it is appropriate to start enrichment in the immediate vicinity of forest reserves or other important refugia of endangered beetles. This will create a backbone network in the sense of a green corridor to more distant localities for easier dispersal of these species into the landscape. As a matter of fact, reserves are not a complex solution in the landscape where an area several times larger is occupied by commercial stands. The proposed management for increasing the biodiversity of saproxylic species reduces timber production. Nevertheless, our concept of active forest management can be classified as Medium-Combined Objective Forestry in the sense of the Duncker et al. ^[127] classification, as it attempts to combine the fulfilment of multiple functions

and needs in a single stand. The absolute amount of loss is influenced by the proposed management parameters, which reflect the tree species. The lowest production loss is in oak because the proposed volume of wood to be left in the stand is the smallest (50 m³/ha for 130 years). In contrast, the highest loss is recorded for beech (150 m³/ha for 100 years). The relative amount of loss in relation to the total volume production is significantly affected by the quality of the site. It varies between 6.3% (oak, SI 34) and 47.3% (beech, SI 18). If we assume that the level of monetization will be the same, then the potential economic loss would be in the range of ca 20 EUR/ha.year (oak) to 45 EUR/ha.year (spruce). However, when applying the recommended methods in the management proposal, a reduction of this loss can be expected due to the preferential leaving of low-value trees to decay. While the economic loss in the application of the proposed model is comparable between sites, the share of this loss in total profit varies considerably, from ca. 10% (SI 30, oak) to ca. 100% (ASI 28, beech). In our case, however, we calculated the actual potential loss by subtracting the estimated costs of harvesting and transporting the wood to the customer from the value of the deadwood left. If we considered only the value of the left wood, we get an amount of 45–70 EUR/ha.year for spruce and beech, and about 30 EUR/ha.year for oak. Moreover, in the poorest beech and oak habitats (SI 14, 18), standard management is unprofitable, so the application of the proposed management in payments for ecosystem services could mean a positive economic outcome and therefore a high incentive for forest owners. These values correspond to the potential ecosystem function of these stands and could be used to derive payments for this service to the forest owner. By comparison, these amounts are equivalent to 20–30% of the flat rate payment in 2020 for agricultural land in the Czech Republic, or 15–25% of the subsidy for organic farming. When applied generally to all commercial forests in the Czech Republic, this would mean an annual payment of approximately 1.9 billion CZK, which corresponds to about 76 million EUR. Still, these financial values are only indicative ones; it is necessary to provide a more precise analysis in a separate economic study.

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